DAY-LENGTH CONTROL OF INFLORESCENCE INITIATION IN THE GRASS *ROTTBOELLIA EXALTATA* L.f.

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Summary

R. exaltata is a strict short-day plant with a critical photoperiod of about 13 hr. The number of short days required for inflorescence initiation varies with age, being 6 with plants 5 weeks old. Exposure to additional short days increases the rate of inflorescence development. The expanding leaf is the one most sensitive to short-day induction and removal of the leaves below it accelerates inflorescence development.

Short-day exposures given to different leaves can, in some cases, be as effective for induction as when the short days are all given to the same leaves.

Long days interpolated between the first two short days of an inductive sequence, or given to the lower leaves early in the inductive sequence while the uppermost leaf blade is exposed to short days, accelerate inflorescence development, while those interpolated or given simultaneously later in the sequence are inhibitory.

It is concluded that short-day leaves produce a stimulus to inflorescence initiation which is translocated from them rapidly after each long night, while long-day leaves produce a transmissible substance which may either accelerate or inhibit inflorescence development depending on the progress toward induction.

I. Introduction

Much recent work on flowering in short-day plants has been concerned with the sequence of partial processes leading to the production, in leaves exposed to short days, of a stable transmissible stimulus to inflorescence initiation. Apart from effects they might have on the movement of this stimulus to the shoot apex, leaves in long days have usually been accorded a neutral role, although several authors (e.g. Schwabe 1956; Guttridge 1959; and Lona 1959) have suggested that they may inhibit initiation in short-day plants. In *Lolium temulentum*, a long-day grass, leaves in short days have been found to produce a transmissible inhibition, and leaves in long days a transmissible stimulus, to inflorescence initiation (Evans 1960), and one of the aims of the present work was to see if a similar dual day-length control of inflorescence initiation operated in a short-day grass.

The other aim was to examine why so many plants need an extended period of induction when some short- and long-day plants require only one inductive cycle. The simplest explanation is that each inductive day produces a subthreshold stimulus to inflorescence initiation, and that these must be added up over a period for induction to occur. It is also possible, however, that there is a sequence of partial processes operating over the period of induction, as there is in each day of it, and some of the results presented here suggest that this may be so. Evidence was also sought of where this summation or sequence takes place—in the leaves which perceive the day-length conditions, or at the shoot apex where differentiation of the inflorescence takes place.

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II. Materials and Methods

Rottboellia exaltata L.f. is a subtropical grass distributed through south-east Asia, India, central Africa, and the West Indies, and naturalized in the Northern Territory of Australia where it flowers in early autumn. Heslop-Harrison (1959) has shown it to be a strict short-day grass in which sex expression and breeding system can be modified by day length. The seed used in the present experiments was from the same collection, from south of Darwin, N.T., as that used by Heslop-Harrison.

Caryopses were sown singly in small plastic pots of perlite, which were given Hoagland's nutrient solution and water daily. The plants were grown in a glasshouse in which the temperature did not fall below 20°C, with the natural day length extended to 18 hr by incandescent lamps, giving illumination of 25 f.c. intensity at plant height. The plants grew rapidly under these conditions, with few lateral shoots, and were remarkably uniform in their rate of leaf appearance and leaf size. On dissection they showed no progress towards inflorescence initiation in 6 months.

Plants of *Rottboellia formosa* R. Br. (C.S.I.R.O. Collection C844) were also grown, and this species was also found to be a strict short-day plant, but its rapid production of lateral shoots and less upright growth habit made it less suitable for the present experiments.

All short-day treatments, unless otherwise stated, consisted of 8 hr at 25°C under natural light followed by 16 hr of darkness at 20°C. The plants were then returned to the long-day glasshouse until 3 weeks from the beginning of the short-day treatment, when the apices of the main shoots were dissected and their lengths and stages of differentiation recorded. Control groups were left in the long-day glasshouse in each experiment, and invariably remained vegetative.

It was hoped to apply to *Rottboellia* the methods developed for *L. temulentum* (Evans 1960) of exposing different leaves simultaneously to either long or short days by wrapping the short-day leaf blades in aluminium foil or by enclosing them in light-tight boxes. Unfortunately, although wrapping or enclosure of leaf blades for single short days can be effective, as will be seen, inflorescence initiation has not been obtained when all short days are given in this way. This could be due to the sheaths of these leaves being in long days, as Chailahjan (1945) and Harder, Westphal, and Behrens (1949) found short-day treatment of the apical half of *Perilla* and *Kalanchoë* leaves to be ineffective when the lower half was in long days. However, in *Pharbitis* (Imamura, Takimoto, and Okuda 1958) and *Begonia* (Esashi 1961) short-day treatment of the apical sections of leaves is effective. In any case, in *Rottboellia* the sheaths of the wrapped upper leaves were wholly enclosed by those of the lower leaves, and the explanation of the inadequacy of leaf wrapping probably lies elsewhere.

Also, removal at intervals of lower leaves in long days during short-day induction could not be used to provide evidence of the movement of inhibitory substances from them since, as will be seen, even removal of the lower leaves during exposures to short days can accelerate inflorescence development.

III. Results

(a) *Number of Short Days Required for Induction*

The effect of exposure of plants with 5–6 leaves on the main shoot to an increasing number of short days can be seen in Figure 1, which includes the results of several experiments. In these there was no inflorescence initiation after exposure to 4 short days, 38–75% initiation after 5, and full initiation after 6. Exposure to more than 6 short days resulted in further increases in the rate of inflorescence development.

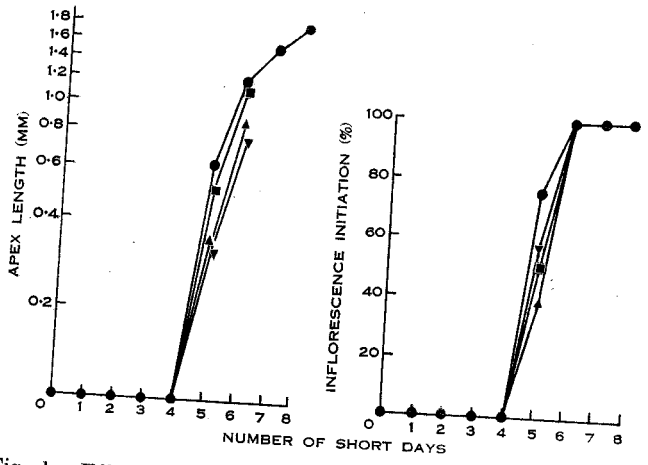

Fig. 1.—Effect of the number of short days on inflorescence initiation and development. ● Plants 34 days old, with only the fifth leaf left, at beginning of short-day treatment; ▼ plants 41 days old, all leaves; ■ plants 42 days old, all leaves; ▲ plants 44 days old, all leaves.

Younger plants require more than 6 short days for induction, and plants 17 days old, with three expanded leaves, were found to need more than 10 short days, while in one experiment with older plants (with nine expanded leaves on the main shoot) 67% of the plants showed inflorescence initiation after exposure to only 4 short days.

In most of the experiments described below plants were used when there were six or seven fully expanded leaves on the main shoot.

That the increased sensitivity to short-day induction with increasing age is not due to increase in the leaf area of the plants is indicated in Figure 1 by the fact that the experiment with the youngest plants, on which only the fifth leaf blade was left, showed the greatest sensitivity.

(b) *Effect of Defoliation*

The effect of removal of the lower leaves just before short-day treatment began on sensitivity to short-day induction was examined in three experiments, the results of which are given in Table 1.

In the first two experiments the uppermost fully expanded leaf and the leaf still expanding were left and all others removed. In both cases removal of the lower leaves significantly increased the rate of inflorescence development, and in the first experiment it also increased the proportion of plants initiating inflorescences.

In the third experiment, removal of all leaves except the uppermost expanded and the still-expanding ones again significantly increased both the rate of inflorescence development and the proportion of plants initiating inflorescences. However, the treatments where only the fully expanded seventh leaf (mean area 83·7 cm² at the beginning of short-day treatment) or the expanding eighth leaf (initial mean area 31·1 cm²) were left on the plants are of greatest interest. When only the eighth leaf

TABLE 1

EFFECT OF REMOVAL OF THE LOWER LEAVES ON THE EFFICIENCY OF SHORT-DAY INDUCTION

Leaves Exposed to Short Days	Number of Short Days	Apex Length (mm)	Inflorescence Initiation (%)
Experiment 1			
All leaves	5	0·25 *	25
Leaves 5 and 6	5	0·62 *	75
Experiment 2			
All leaves	6	1·17 *	100
Leaves 7 and 8	6	2·17 *	100
Experiment 3			
All leaves	6	0·54	50
Leaf 7	6	0·59 **	62·5
Leaves 7 and 8	6	1·28 **	100
Leaf 8	6	2·04 **	100

* Difference significant at $P<0·05$.

** Difference significant at $P<0·01$.

was present during short-day treatment, the rate of inflorescence development was significantly greater than when both seventh and eighth leaves were present. The presence of the seventh leaf has therefore partially inhibited the response to the eighth leaf, although alone it permitted a slight response to short-day treatment. *Rottboellia* thus resembles *Xanthium* in that it is the expanding leaf which is most sensitive to short-day induction (Khudairi and Hamner 1954), but differs from it in the inhibitory effect of the lower leaves.

Total defoliation of plants held in long days has never resulted in inflorescence initiation, and in this respect *Rottboellia* differs from the strawberry (Thompson and Guttridge 1960).

(c) *Response to Day Length*

Plants held from germination in photoperiods of 16 or 18 hr, or in continuous light, have never initiated inflorescences. On the other hand, plants held in 8-hr photoperiods from germination have initiated inflorescences: eight plants dissected 8 weeks after germination all had inflorescences in an advanced stage of differentiation, of 2·15 cm mean length. Other groups of plants sown at the same time, but given 1, 2, or 3 weeks in 18-hr days before exposure to 8-hr photoperiods, had mean inflorescence lengths of 1·65, 0·94, and 0·52 cm respectively when dissected at the same time as the group held in short days throughout. It is clear then that *R. exaltata* is a strict short-day plant, and that even in the earliest stages of growth short days hasten inflorescence initiation and development.

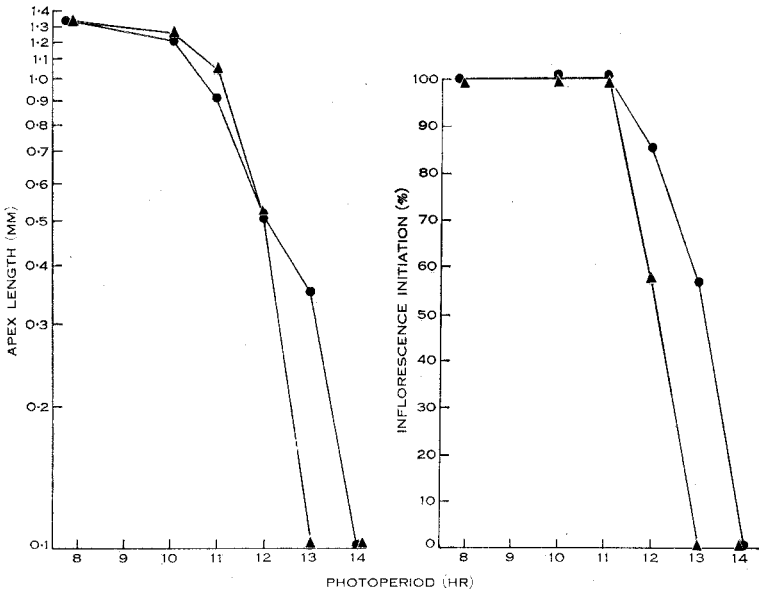

Fig. 2.—Effect of day length during the first (●) or the last (▲) 2 days of exposure to 6 consecutive short days on subsequent inflorescence initiation and development.

In order to determine the day-length response curve, and whether this altered with the progress of induction, a group of plants 5 weeks old, with the sixth leaf fully expanded, was removed from the long-day glasshouse for exposure to 6 short days at various photoperiods. The short-day treatments were given in a series of controlled-environment cabinets all at 25°C under natural light for 8 hr followed by 16 hr at 20°C, in darkness or with extensions to the photoperiod by incandescent illumination of 40 f.c. intensity. In one series of treatments the photoperiod during the first 2 days was either 8, 10, 11, 12, 13, or 14 hr, the following 4 days all having 8-hr photoperiods. In the other series the photoperiod for the first 4 days was 8 hr, while for the following 2 days it was either 8, 10, 11, 12, 13, or 14 hr. There were seven plants in each treatment, and all had the lower leaves removed and only the

sixth leaf exposed to short days in order to increase their sensitivity to induction. The results of the dissections are given in Figure 2.

It can be seen that photoperiods of 14 hr were ineffective for induction, while those of 13 hr were effective only when given during the first 2 days. 12-hr photoperiods were effective at both the beginning and end of the short-day treatment, but more so at the beginning. At shorter photoperiods initiation occurred in all plants, but the rate of inflorescence development increased with shortening of the photoperiod to 8 hr.

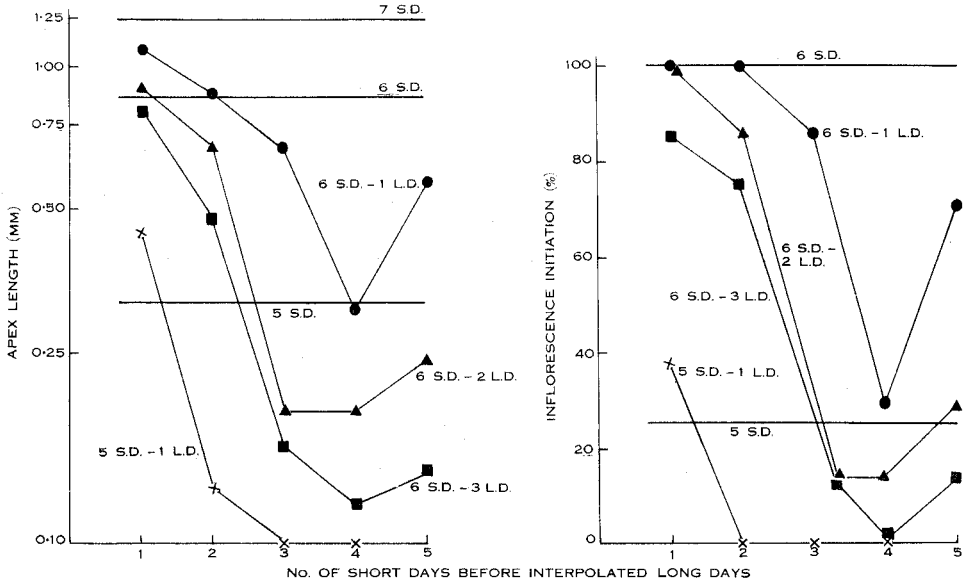

Fig. 3.—Effect of interpolating 1 (●), 2 (▲), or 3 (■) long days into a sequence of 6 short days, or 1 long day into a sequence of 5 short days (×), on subsequent inflorescence initiation and development. Horizontal lines indicate development when no long days were interpolated.

(*d*) *Interpolation of Long Days in an Inductive Sequence*

In order to determine the effect of long days interpolated during short-day induction, plants with the sixth leaf fully expanded, and with all leaves left on them, were given either 5 or 6 short days, groups of these being given up to 3 days in 18-hr photoperiods at various positions in the inductive sequence. There were eight plants in each treatment.

Results of the dissections are given in Figure 3, which shows the marked influence of the position in the inductive sequence when the long days were interpolated. Whereas a long day given after the first short day of the sequence of either 5 or 6 short days hastened inflorescence development, those interpolated later in the sequence had a marked inhibitory effect, which was greatest for those given after 4 short days. This inhibitory effect increased with increase in the number of interpolated long days with the result that 3 long days given after the fourth short day completely suppressed inflorescence initiation.

This pattern of results was reproduced almost exactly in a further experiment, the inhibitory effect of later interpolations being highly significant in all cases. Table 2 sets out the effects of giving one long day after the first short day of an inductive sequence, and it can be seen that in all three experiments this has resulted in an increased rate of inflorescence development. Although the increases in apex length just failed to reach the 5% probability level in each experiment, taken together they may represent a real stimulation of inflorescence development.

TABLE 2

EFFECT OF INTERPOLATION OF A LONG DAY AFTER THE FIRST SHORT DAY OF AN INDUCTIVE SEQUENCE

L, long day; S, short day

Photoperiodic Treatment	Apex Length (mm)	Inflorescence Initiation (%)
S, S, S, S, S	0·32	25
S, L, S, S, S, S	0·45	38
S, S, S, S, S, S	0·86	100
S, L, S, S, S, S, S	1·08	100
S, S, S, S, S, S	1·17	100
S, L, S, S, S, S, S	1·41	100

(e) *Simultaneous Exposures to Long and Short Days*

The inhibitory effect of interpolated long days is not necessarily due to the production of a transmissible inhibitor since it could also be caused by decay or dilution of the previously accumulated short-day stimulus. The latter explanation could be ruled out, however, if leaves in long days, below those undergoing short-day induction, could be shown to be inhibitory.

Plants with the seventh leaf fully expanded were removed from the long-day glasshouse for exposure to 6 consecutive short days. All leaves were left on the plants, and in the short-day control group all leaves were exposed to the 6 short days. In the treatment groups, each of eight plants, however, all leaves other than the seventh were exposed to one long day by placing the plants in an 18-hr photoperiod at various times during the inductive sequence, and during these long-day exposures the blade of the seventh leaf was wrapped in aluminium foil. Results of the dissections 3 weeks later are given in Table 3.

It is clear that the effect of long days given to the lower leaves during short-day treatment depends markedly on their position in the inductive sequence, as it did when they were interpolated in it. The pattern of effects is also broadly similar in that long days given simultaneously with short days toward the end of the inductive sequence were most inhibitory, while those given earlier increased both the length

and the stage of differentiation of the inflorescence. In this experiment, the accelerating effect on inflorescence development was highly significant, and was most marked after the second short day, whereas with interpolated long days it was apparent only after the first short day.

(*f*) *Effect of Short Days Given to Different Leaves*

In order to determine where summation of the response to a series of short days occurred—in the leaves exposed to them or at the apex where the inflorescence differentiates—several experiments were carried out in which the 6 short days required for induction in standard plants were given consecutively but to different

TABLE 3

EFFECT OF HAVING THE LOWER LEAVES IN LONG DAYS AT VARIOUS TIMES THROUGHOUT THE PERIOD WHEN THE UPPERMOST LEAF IS IN SHORT DAYS

L, long day; S, short day

Photoperiodic Treatment	Apex Length (mm)	Inflorescence Initiation (%)
All leaves : S, S, S, S, S, S	1·17	100
Leaf 7 : S, S, S, S, S, S Leaves 1–6: S, L, S, S, S, S	1·30	100
Leaf 7 : S, S, S, S, S, S Leaves 1–6: S, S, L, S, S, S	1·77**	100
Leaf 7 : S, S, S, S, S, S Leaves 1–6: S, S, S, L, S, S	1·22	100
Leaf 7 : S, S, S, S, S, S Leaves 1–6: S, S, S, S, L, S	0·77*	63

* Significantly different from plants with all leaves in all short days at $P<0·05$; ** at $P<0·02$.

leaves. Single short days given to each of the six leaves on the main shoot consistently failed to yield any induction, as did 2 short days given to each of the three uppermost leaves. Giving the first 2 or 4 short days to the uppermost leaf, and the remaining 4 or 2 to the one below it also failed. These negative results could mean that the effect of short-day exposures is not additive when they are given to different leaves, but they could also be due to the limited adequacy of short-day exposures obtained by wrapping the leaf blades in aluminium foil, as noted above.

In two experiments summation of the effects of short days given to different leaves has been obtained, and the results of these are given in Table 4. In both cases

the successful summations have been obtained when the first short day was given to the uppermost leaf blade by wrapping it in aluminium foil while the plants were held in long days, the wrapped leaf blade then being cut off before the lower leaves were exposed to the other 5 long nights. In one experiment the time when the uppermost leaf blade was cut off was varied, and it is clear from the results that even when the leaf blade was removed immediately at the end of the first long dark

TABLE 4

EFFECT OF GIVING THE FIRST SHORT DAYS TO THE UPPERMOST LEAF WHILE THE LOWER LEAVES ARE IN LONG DAYS, OTHER SHORT DAYS TO THE LOWER LEAVES, AND OF TIME OF REMOVAL OF THE UPPERMOST LEAF AFTER THE FIRST LONG NIGHT

L, long day; S, short day

Photoperiodic Exposure	Time of Removal of Leaf 7	Apex Length (mm)	Inflorescence Initiation (%)
Experiment 1			
All leaves : 5S	—	0·11	0
All leaves : 6S	—	0·53	80
Leaf 7 : S Leaves 1–6: L, 5S	4 p.m. (I)	0·45	83
Leaf 7 : 2S Leaves 1–6: 2L, 4S	4 p.m. (II)	0·10	0
Experiment 2			
All leaves : 5S	—	0·50	50
All leaves : 6S	—	1·17	100
All leaves : S, L, 5S	—	1·41	100
Leaf 7 : S Leaves 1–6: 2L, 5S	9 a.m. (I)	1·48	100
	12 noon (I)	1·25	100
	4 p.m. (I)	1·22	100

period, sufficient of the stimulus to inflorescence initiation has been translocated from it for full initiation to occur and for the subsequent rate of inflorescence development to be at least as rapid as in plants in which all leaves were exposed to all short days. In fact, the longer the leaf blade given the first short day was left on the plant the lower was the rate of inflorescence development, but this trend was not statistically significant.

IV. Discussion

(a) *Inhibitory Effect of Long Days*

Where short-day plants require several short days for the initiation of flowering it has often been found that groups of short days each with less than the threshold number separated by interpolated long days can yield flowering plants (Carr 1955). The fact that the effect of the separated short days is often less than the effect of the same number given consecutively has usually been attributed to decay or dilution of the short-day stimulus during growth in the interpolated long days. Carr (1955) suggested that it might also be due to an inhibitory effect from the interpolated long days.

Schwabe (1956, 1959) examined the effects of long days interpolated during short-day induction, mainly in *Kalanchoë*, and he concluded that interpolated long days have a positive inhibitory effect, which is additive when the long days are given singly, each long day annulling the effect of about 2 short days. The validity of this relation is dubious, however, since, as Schwabe (1956) also found, the effect of a long day depends on when it is interpolated in the inductive sequence. He further concluded that the inhibitory effect of interpolated long days is exercised on the effect of the short days following them, rather than on the preceding ones. This conclusion is based on the results of experiments in which supposedly "neutral" dark periods of 24 hr duration were interposed between the long and the short days. But in no sense can such a dark period be considered photoperiodically neutral, and the results Schwabe (1959) presents on the effect of temperature during these dark periods indicate clearly that they are not so.

The inhibitory effects of interpolated long days obtained by Schwabe (1959) with *Kalanchoë* and other short-day plants, and here with *Rottboellia*, could be caused by the decay or dilution of the previously accumulated short-day stimulus during the interpolation. However, this explanation does not account for the inhibitory effect of exposing the lower leaves of *Rottboellia* to one long day while the uppermost leaf was exposed to the fifth short day of the inductive sequence (Table 3). Since the long-day leaves were below those in short days their inhibitory effect is unlikely to be due to their acting as sinks for the stimulus from the short-day leaves (Lang 1952), but rather to the production of a transmissible inhibitory substance.

The results of selective defoliation treatments established that the lower leaves may also be inhibitory when held in short days. Preliminary experiments in which the lower leaves were removed at various times during short-day treatment, leaving only the seventh and eighth leaves, have shown that this inhibitory effect also becomes more marked towards the end of the short-day treatment. Thus, the lower leaves are increasingly inhibitory to inflorescence initiation in *R. exaltata* the longer they are left on the plant during the short-day induction period, whether held in long or short days. But they are far more inhibitory when held in long days, as may be seen from Table 3.

Guttridge (1959) has also found evidence of a transmissible inhibition to flower initiation from long-day leaves in the strawberry, and Thompson and Guttridge

(1960) were even able to obtain flower initiation in continuous light by defoliating their plants. In this facultative short-day plant, then, a requirement for a positive stimulus to initiation from short-day leaves is not apparent, whereas in *Rottboellia* a dual control of inflorescence initiation by day length, like that in *Lolium temulentum* (Evans 1960), appears to operate, short-day leaves producing a stimulus to initiation and long-day leaves an inhibitor, these both being transmissible and presumably interacting at the shoot apex.

Esashi (1961) has found a similar dual control by day length of the initiation of aerial tubers in *Begonia evansiana*, while the results of Bogorad and McIlrath (1959) suggest that a similar system may control inflorescence initiation in *Xanthium pennsylvanicum*. Such dual control could increase the sensitivity of responses to photoperiod near the critical day length. It could also confer a degree of temperature independence on the photoperiod response when the promotive and inhibitory processes are similarly affected by temperature.

(*b*) *Movement of the Short-day Stimulus*

Evidence that the stimulus from short-day leaves is transmissible is provided by the results in Table 4, where removal during the following day of the only leaf blade exposed to the first long night of an inductive sequence incurred no reduction in the rate of inflorescence development. That this was so, even when the leaf blade was cut off at the time of unwrapping, indicates that translocation of the short-day stimulus can occur during the dark period.

This finding is of interest not only because it indicates translocation of the stimulus from the short-day leaves, but also that this can occur after only 1 short day although at least 5 short days are required for induction. This strongly suggests that the stimulus is summated at the apex rather than in the leaf, and that it is the shoot apex and not the leaf exposed to short days which is induced in *Rottboellia*. In this respect it resembles *Xanthium* and soybean (Carr 1953) but not *Perilla*, in which detached leaves can be induced (Lona 1949).

(*c*) *Action at the Apex*

Given accumulation at the apex of at least two transmissible substances affecting induction, several modes of operation might be envisaged for them:

(1) The stimulus translocated to the apex after each short-day exposure could, in the absence of any long-day inhibition, be converted to a final stable product which must attain some threshold concentration for induction to occur. The marked heterogeneity of the inductive period, indicated by the very different effects of long days interpolated or given simultaneously at various points in the inductive sequence, does not support this suggestion.

(2) The short-day stimulus could accumulate at the apex until a threshold concentration is reached when, in the absence of long-day inhibition, the final process leading to induction is consummated. The fact that the inhibitory effect of long days, interpolated or given simultaneously during induction, increases the later they are given in the inductive sequence,

reaching a maximum at the time the threshold short day is given, supports this interpretation. One would expect, however, that any reduction in leaf area exposed to short days, or any experience of long days during induction, would reduce initiation and the rate of inflorescence development, whereas the reverse is the case.

(3) The substances translocated from the leaves exposed to both short and long days participate in induction in *Rottboellia*, the most favourable balance between them changing as induction proceeds.

Chailahjan (1958) has developed an ingenious theory for the control of flowering in all plants by two such groups of substances. His theory could be extended to account for the inhibitory action of non-inductive conditions in both long- and short-day plants with the additional assumption that it is the balance between the two groups of substances which determines the morphogenic outcome, as it may do with auxin and kinetin (Skoog and Miller 1957). The promotive effect of long days interpolated or given simultaneously early in the period of induction would then indicate that the stimulus from the short-day leaves may be received in excess in the early stages of induction by 8-hr photoperiods. Were this so, the optimum photoperiod length should be more than 8 hr during the early exposures to short days. The results given in Figure 2 give no indication of this, although the upper limit for photoperiod length effective in induction is longer during the first two days than during the last two.

In the absence of evidence for an excess of the short-day stimulus early in induction, one is forced to conclude that the substances translocated from long-day leaves, while usually inhibitory to inflorescence initiation, may participate in early phases of the inductive process. However, exposure to long days is not essential for either the initiation or the development of inflorescences in *R. exaltata*.

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